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REVIEW

Competition between marine mammals and fisheries in contemporary harvested marine ecosystems

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ABSTRACT: Competitive interactions between marine mammals and fisheries represent some of the most complex challenges in marine resource management worldwide. The development of commercial fisheries and recovering marine mammal populations have contributed to a decrease in fish availability. Whilst ecosystem-based fisheries management (EBFM) can counteract this decrease, achieving the EBFM objectives faces certain major obstacles including insufficient or unreliable data, inapplicable assessment models, as well as inadequate management decisions that do not account for fisheries-induced morphological alterations (FIMA) and marine mammal management. Despite a body of evidence addressing various aspects of marine mammal–fisheries competition, little is known about the effects of marine mammal–fisheries biological interactions affecting the fish viability and food web stability. We review the research on marine mammal–fisheries competitive biological interactions (hereafter biological competition) by focussing on (1) the prerequisites for marine mammal–fisheries biological competition and the relevant methodologies to explore them and (2) recent studies revealing the implications of FIMA and trophic interactions for the biological competition. We also discuss the implications of FIMA, eco-evolutionary feedback and prey–predator dynamics for EBFM implementation in contemporary harvested ecosystems. Our main findings reveal a lack of data about marine mammals' prey choice and selectivity, the need for better representation of marine mammals in modelling approaches and lastly, the necessity for additional research linking FIMA, trophic interactions and the EBFM objectives. To conclude, interdisciplinary approaches may serve to link all of the efforts needed to effectively and holistically support the implementation of EBFM.

KEY WORDS: Resource competition · Fisheries · Cetacean · Pinniped · Prey–predator dynamics · Ecosystem-based management · Fisheries-induced

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1. INTRODUCTION

Many contemporary harvested marine ecosystems are often characterised by competitive interactions between humans and marine predators (Pauly et al. 1998, Trites et al. 2006). From this aspect, realising sustainable long-term yields in fisheries requires an

in-depth understanding of the impact these interactions have on fish survival and the ecosystem. In this article, we attempt to review this information in the published and available material and address this issue while considering the morphological alterations observed in fish under intensive fishing as well as the overall implications for ecosystem-based man-

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agement. As an introduction to the topic, we first briefly present a historical overview of marine mammal–human non-competitive and competitive interactions, then describe the main impacts and roles of marine mammals and fisheries in the ecosystem and their management. We conclude by defining marine mammal–fisheries competition as well as the aim and structure of this literature review.

1.1. Brief historical overview of competitive interactions between humans and marine mammals

The human exploration of marine ecosystems in search of food stands as a key moment preceding the competition between fisheries and marine mammals for fish (Lavigne 2003). The oldest archaeological findings of fishing tools, dating to 8800 BC, provide evidence for the beginning of the development of fishing activity. Some of the oldest evidence for marine fishery-dependent communities have been found in Crete (6000 BC), and in Egypt around 2000 BC, fishing activity was highly associated with social status (Lackey 2005). Accompanying global technical and technological development, the diversification and development of fishing gear, vessels and fish preservation techniques facilitated the expansion of fishing areas towards open waters (Jackson et al. 2001, Lackey 2005). Over time, interactions between humans and marine mammals diverged into 2 interchangeable and often mutually non-exclusive types. The first type of interaction consisted of humans depending upon marine mammals as a natural resource, while the second type consisted of the perception of marine mammals as a direct threat to humans' livelihoods and tradition. The first type of interaction did not necessarily consist of competition, although it might have developed due to an initial competitive interaction. Whether non-competitive or competitive, marine mammal–fisheries interactions significantly impacted the historic abundance of marine mammals.

Countries in the Northern Hemisphere, such as Norway, Iceland, Denmark, Russia, Canada and the USA, have traditionally hunted whales for oil, baleen and meat whilst also hunting seals for their fur and meat (Tønnessen & Johnsen 1982, Ellis 1991, Harding & Härkönen 1999, Reeves & Smith 2006). In addition, sea otters *Enhydra lutra* were hunted for their fur along the North Pacific coastal waters of Russia, Canada and the USA (e.g. California and Alaska; Kenyon 1969, Bodkin 2015). Until the enactment of federal protection laws in the 1970s, sea otters were

nearly brought to extinction through hunting programmes in California and Alaska (Carswell et al. 2015). Today, much effort is put into the management of this small, yet economically and ecologically important marine mammal species (Carswell et al. 2015, Estes 2015).

In the case of commercial whaling, a moratorium proposed by the International Whaling Commission (IWC 1946) has limited the removal of baleen whales since 1986, although Norway and Iceland were exempted and continued to hunt minke (*Balaenoptera acutorostrata*) and fin (*Balaenoptera physalus*) whales (see Howell & Bogstad 2010), establishing their own quotas. Based on 2017 whale catches (www.iwc.int), the approximate proportions of commercial whaling, aboriginal subsistence and special permit stood at 33, 24 and 43 %, respectively. Furthermore, whaling practices still remain a tradition in some countries, such as Iceland, Norway (IWC 2016) and the Faroe Islands (Singleton & Fielding 2017), whereas aboriginal subsistence whaling is allowed for several indigenous communities in Alaska (USA), Chukotka (Russia), the West Indies (St. Vincent and the Grenadines) and Greenland (Denmark; Gambell 1993, Reeves 2002). Thus far, 'scientific whaling' has been conducted by the Japanese fleet in Antarctic waters (Kalland & Moeran 2010, IWC 2016). However, recent (December 2018) announcements by the Japanese government disclosed their intention to leave the IWC and begin whaling in Japanese jurisdictional waters, whilst ceasing to hunt in Antarctic waters. Additionally, 'bycatch' minke whales are being commercialised in South Korea (MacMillan & Han 2011, Tatar & Jung 2018).

Competitive interactions for fish have reportedly led to occasional retaliations from fishermen against marine mammals, ultimately contributing to the introduction of the intentional removal (namely culling) of many marine mammal species (DeMaster et al. 2001, Kaschner & Pauly 2005). In the Mediterranean Sea, for example, cullings were recorded as early as the sixteenth century (Bearzi et al. 2004, 2009). This marked the beginning of a long period of dolphin removals persisting until the end of the twentieth century, leading to significant declines of Mediterranean and Black Sea bottlenose (*Tursiops truncatus*) and short-beaked common (*Delphinus delphis*) dolphins (Mitchell 1975, Holcer 1994, Birkun 2002, Bearzi et al. 2004, 2009). Similar culling events occurred along the Atlantic coastlines of Spain and Norway (Øien 1988, Valdés 2004). Specifically, cullings of Iberian populations of small cetaceans in the northeast Atlantic lasted for centuries (Valdés 2004, 2009), whilst in

Norway, the culling of killer whales *Orcinus orca* followed the population collapse of herring *Clupea harengus*, which had resulted primarily from over-fishing (Øien 1988). The culling of small cetaceans in Europe did not represent unique culling events, particularly given events in Japan (Kasuya 1985).

Pinniped species such as grey (*Halichoerus grypus*) and ringed (*Histriophoca fasciata*) seals were heavily hunted by several Baltic countries for their fur, but, more importantly, also because of their competition for cod *Gadus morhua*, herring and sprat *Sprattus sprattus* fisheries (Harding & Härkönen 1999, Hansson et al. 2007). In the northeast Atlantic, grey and ringed seals were also culled in UK, Norwegian and Icelandic waters (Bowen & Lidgard 2013), whilst Scotland and Iceland undertook cullings of harbour seal *Phoca vitulina*. Beyond European waters, primarily in the USA and Canada, pinniped species, such as California sea lions *Zalophus californianus*, northern sea lions *Callorhinus ursinus*, harbour seals and Steller sea lions *Eumetopias jubatus*, were culled (Bowen & Lidgard 2013). Sea otters were perceived as a direct competitor for Alaskan and Californian shellfish fisheries (including various bivalves, sea cucumbers and crab species) which, in addition to the fur trade, supported sea otter cullings (see Erlandson et al. 2005, Carswell et al. 2015).

Owing to various international laws and regulations (e.g. IWC regulations), retaliation or unregulated kills of marine mammals are now illegal, although a large proportion of marine mammal mortality (especially for small cetaceans) stems from unintentional removals or bycatch (Northridge & Hofman 1999, Read et al. 2017). However, when compared to numbers recorded during the historic commercial whaling typical of the twentieth century and seal hunting by indigenous nations, marine mammal populations appear to be steadily recovering (IWC 2016). This observation does not hold for all marine mammal species, but primarily applies to baleen whales and some seal species (Read & Wade 2000). Other marine mammal species, however, have not significantly recovered, perhaps hampered by other emerging threats (e.g. bycatch, pollution, diseases; Roman et al. 2013, IWC 2016).

1.2. Marine mammals and fisheries: relation to EBFM in contemporary marine food webs

Marine mammals have a wide range of trophic niches. As key species in various marine ecosystems, they play a crucial role in underlying ecological pro-

cesses that preserve ecosystem functioning (see Bowen 1997, Pauly et al. 1998). Marine mammals contribute to both top-down and bottom-up control through trophic interactions. With respect to top-down control, the consequences of removing the top predators normally precedes an increase in meso-consumers in the trophic web as well as a decrease in the lower trophic level such as in foraging fish, detritivores and grazers (Heithaus et al. 2008, Roman et al. 2014). Marine mammals may also exert a bottom-up control in a trophic web contributing to an ecosystem's productivity through the defecation of iron- and nitrogen-rich excreta. This reportedly holds true for coastal ecosystems, where cetaceans and pinnipeds forage and feed, notably stimulating primary production through defecation as well as distributing and dispersing nutrients due to their rapid ascent and descent (Roman & McCarthy 2010, Lavery et al. 2014, Roman et al. 2014). In oceanic ecosystems, the mixing of nutrients correlates more strongly with baleen and large toothed whales (see Roman & McCarthy 2010), owing to their size and diving abilities. While marine mammals directly affect the abundance of target species, their indirect effects crucially boost ecosystem productivity. Thus, some studies suggest that, in their role as top predators and ecosystem engineers, marine mammals facilitate rather than harm fisheries, strengthening their concomitant economies in the long term (see Yodzis 2001, Gerber et al. 2009, Morissette et al. 2012, Lavery et al. 2014, Roman et al. 2014).

In agreement with the theory of trophic interactions, fisheries can operate at the same trophic level as top predators, albeit causing severe adverse effects observed at all structural levels (Trites et al. 2006, Daskalov et al. 2007). In contrast to marine mammals that co-evolve with their prey, developing a specialisation in prey choice or becoming rather indiscriminate in terms of prey preferences (Trites et al. 2006), fishing tools are primarily size selective, targeting mostly large and economically valuable fish (Heino & Dieckmann 2008). Considering the amount of fisheries uptake, such selective removal can cause negative changes in the life-history traits of the target species in the long-term, including declines in body size and the age of maturation, potentially, in turn, negatively affecting the fecundity and viability of the fish population (Sharpe & Hendry 2009, Wright & Trippel 2009, Kuparinen et al. 2014). Some studies have indicated that through persistent intensive fishing, such fisheries-induced morphological alterations (FIMA) can lead to increased fluctuations in recruitment (Anderson et al. 2008), for in-

stance, negatively affecting fisheries catches as well as fish stock recovery (Enberg et al. 2009). By contrast, while marine mammal species can also exhibit a specific prey size preference (e.g. as observed in seal and cetacean species), their prey choice does not strictly depend upon prey size, instead extending to intra- and interspecific competition and the ecosystem's carrying capacity (see Lindeberg & Pyenson 2006). These differences between fisheries and marine mammals will be expanded upon and further discussed in the relevant sections below.

The overexploitation of fish stocks spurred by the industrialisation of fisheries has exhausted a number of diverse marine ecosystems (Jackson et al. 2001) and contributed to, *inter alia*, the global stagnation of fisheries landings in the 1980s (Pauly et al. 2002, Trites et al. 2006, FAO 2016). As a response to depleted yields, the primary measures employed in fisheries management have focussed on technological improvements to fishing tools rather than the better acquisition of field data, analysis of the situation and identification of the causes of fish decline as proposed by the scientific community. Moreover, in certain fisheries-dependent communities, this situation yet again ignited older criticisms of marine mammals. This hampered the comprehensive and thorough analysis of the situation that took anthropogenic factors potentially contributing to the declines in fish catches into account, such as an unsustainable fishing intensity, illegal fishing activities and the disregard of various fishing regulations (Kaschner & Pauly 2005, Gerber et al. 2009). For fish and marine mammals, a prolonged state of overexploited fishing stocks can postpone or entirely impede fish stock recovery (Hutchings 2000) as well as diminish the chances of marine mammal survival through longer periods of starvation (see Esteban et al. 2016).

In response to contemporary threats to fishing sustainability and the functioning of marine ecosystems, a holistic approach to marine resource management is needed (Botsford et al. 1997). Ecosystem-based fisheries management (EBFM) represents a managerial approach that consolidates human and environmental well-being (Link 2002, Pikitch et al. 2004). The effective implementation of EBFM requires an understanding of ecosystem processes, the direct and indirect impact of fisheries on the ecosystem, the preservation of trophic interactions considering the top predators competing for the same fish as fisheries, as well as the application of effective approaches accounting for uncertainties about prey–predator dynamics (see Constable 2011). Whilst various case studies and attempts at implementing

EBFM exist, it is clear that the application of knowledge and particularly, recent insights into the dynamics of marine mammal–fisheries competition play important roles in reaching EBFM-related goals. Therefore, a detailed discussion of fish–marine mammal dynamics within harvested ecosystems and its significance for EBFM implementation will be further addressed in the relevant sections below.

1.3. Defining marine mammal–fisheries biological competition

Understanding competition between marine mammals and fisheries is not as straightforward and intuitive as one might assume (DeMaster et al. 2001, Kaschner & Pauly 2005). In total, 11 species of baleen whales, 63 species of toothed whales, 31 pinniped species, and 1 otter species reportedly interact with fisheries in various ways (King 1964, Jefferson 1993). Previous studies have elaborated upon definitions and implications of marine mammal–fisheries competition (Trites et al. 1997, 2006, Matthiopoulos et al. 2008), whereby each addressed different aspects of the competition, highlighting certain shared prerequisites necessary for marine mammal–fisheries competition to occur. In particular, these entail the exploitation of the same resource with notable temporal and spatial overlap, whilst the competitive nature of the interaction suggests that one competitor's gain in resource results in another's loss (also known as the 'surplus-yield' concept). Furthermore, competition between marine mammals and fisheries encompasses 2 types of interaction: operational and biological (Fig. 1) (Northridge & Hofman 1999, Goldsworthy et al. 2003). Operational interactions are the most obvious type of marine mammal–fisheries interaction, referring specifically to marine mammal interference with fishing activities, primarily fishing gear (e.g. depredation; Goetz et al. 2014). Biological (or ecological) interactions (hereafter biological competition) can be direct, whereby fisheries and marine mammals evidently target the same resource (Goldsworthy et al. 2003). Apart from direct interactions, indirect biological interactions (i.e. 'the food-web competition') occur at the level of primary production, cascading throughout the entire food web and reflecting the organic production necessary to sustain both competitors (Trites et al. 1997, 2006).

Biological and operational competitive interactions between marine mammals and fisheries are rarely observed separately. In this context, insights gained

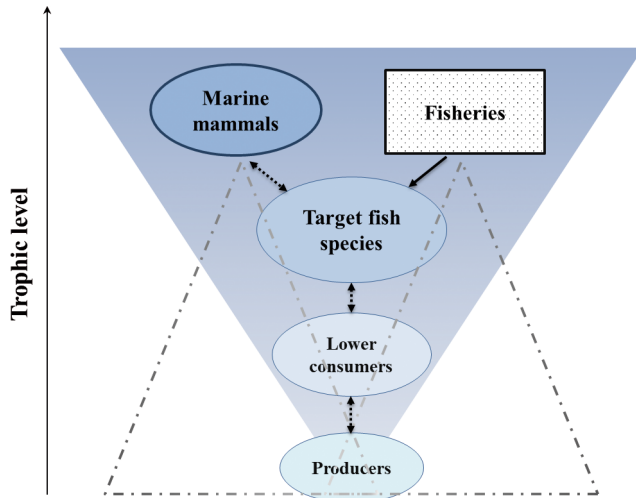


Fig. 1. Trophic levels in marine ecosystems increasing from producers to top predators and fisheries, adapted from Trites et al. (1997, 2006). Transient blue triangle: extent of direct competition between fisheries and marine mammals; dotted-line grey triangles: indirect or 'food-web' competition with a clear lack of resource overlap between the 2 top competitors; 2-way dotted arrows: direction of trophic interactions between the main trophic groups; one-way arrow: direction of fisheries' impact on the target fish species

from research on biological interactions complement our understanding of operational interactions, whereas the opposite does not always apply. The challenges lie in identifying and measuring direct and indirect biological competition which requires special attention, since the effects of marine mammal–fisheries biological competition are latent and can potentially accumulate across trophic levels and over time. For instance, if one observes this from an individual level, where different prey experience different predation pressures due to their individual variability (e.g. sex, age, developmental stage or health status), any change or lack of synchronicity in prey–predator dynamics resulting from that individual variability in responses will inevitably affect the strength and impact of biological competition. Inadequately managed or unaccounted for shifts and disruptions in the dynamic ecological processes governing an ecosystem could lead to its dysfunctionality. Thus far, previous studies addressing marine mammal–fisheries competition have examined the impact and significance from the perspective of principles and assumptions of trophic-interaction theory (e.g. DeMaster et al. 2001), the development of methodological approaches (Kaschner & Pauly 2005, Matthiopoulos et al. 2008), the importance of biological interactions and ecological complexity (Harwood & McLaren 2004, Pierce et al. 2004, Kaschner & Pauly 2005, Matthiopoulos et al. 2008) and the need for

more effective and interdisciplinary conservation measures (Bearzi 2007, Leslie & McLeod 2007).

Therefore, this article aims to review and synthesise existing knowledge gained from studies exploring biological competition between marine mammals and fisheries targeting the same fish species. Since marine mammals comprise species originating from different taxonomic groups (cetaceans [order Cetacea], pinnipeds [superfamily Pinnipedia], the otter family [Mustelidae], sirenians [order Sirenia] and polar bears [family Ursidae]), we specifically address the interactions between fisheries and cetaceans, pinnipeds and sea otters, given that these appear to interact most often with fisheries. Furthermore, in this review we first combine the existing knowledge of the prerequisites of marine mammal–fisheries biological competition, presenting a cross-section of relevant information and methods used in research on marine mammal–fisheries biological competition. Next, we provide insights into recent studies highlighting the implications of FIMA for marine mammal–fisheries biological competition at the individual and population levels and discuss how FIMA, eco-evolutionary processes and prey–predator dynamics affect the implementation of the EBFM objectives. By disentangling the issue of marine mammal–fisheries biological competition, we strive to better describe the potential consequences of biological competition, not simply to achieve sustainable fisheries. That is, we also aim to better link marine resource exploitation and conservation through the implementation of evidence-based recommendations concerning ecosystem functioning for contemporary harvested ecosystems.

2. METHODOLOGY

We conducted a literature search focusing on 2 specific areas:

- (1) existing knowledge and methodology relevant for understanding marine mammal–fisheries biological competition;
- (2) recent insights into implications of prey–predator dynamics experiencing FIMA and their relevance for marine mammal management as well as the EBFM objectives.

We collected the relevant published literature (including journal articles, reviews, PhD theses, technical reports and conference papers) through extensive literature searches performed in 2018 that were focussed on these 2 specific areas. We used the Google Scholar, Scopus, ScienceDirect and Ovid search en-

gines for our literature search. In these literature searches, manuscripts published from 2000 through 2017 were considered in an attempt to capture the most recent research on the above topics. The searches were not limited by geographical area or language, although English was applied in all search engines. References were consulted in all of the papers selected, and we included papers based on the significance of their findings for the focus areas and the selection criteria rather than year of publication.

We performed 3 independent literature searches to address the knowledge and case studies on marine mammal–fisheries interactions as well as the 2 specific areas. The selection of literature collected from all searches relied on the manuscript title and abstract screening. For the first literature search, we used random combinations of the following keywords: ‘marine mammals’, ‘fisheries’, ‘competition’, ‘pinniped’, ‘cetaceans’, ‘sea otter’, ‘conflicts’, ‘marine predator’ and ‘food web’. This initial wide literature search allowed us to define specific systematic categories (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m627p207_suppl.pdf).

The second literature research was done to complement the first and specifically to address the first specific area. Here, we used random combinations of these keywords: ‘cetaceans’, ‘pinnipeds’, ‘sea otter’, ‘fisheries’, ‘competition’, ‘observations’, ‘diet’, ‘feeding ecology’, ‘modelling’, ‘consumption’ and ‘ecosystem dynamics’. The third literature search was conducted to address the second specific area using random combinations of the following keywords: ‘marine mammals’, ‘fisheries’, ‘competition’, ‘pinniped’, ‘cetaceans’, ‘sea otter’, ‘ecosystem-based’, ‘community’, ‘conservation’, ‘fisheries-induced’ and ‘interdisciplinary’.

We selected the collected literature from all searches according to specific selection criteria with respect to 2 focus areas. Selection criteria supporting the first focus area included (1) studies and their respective methodology that contributed to an understanding of spatial, temporal and resource overlap between marine mammals and fisheries; (2) marine mammal dietary studies; and (3) model-based approaches that incorporated marine mammal–fisheries biological competition. The selection criteria supporting the second focus area encompassed studies addressing (1) the effects of FIMA on the individual fish traits and their consequences for prey–predator dynamics; (2) how FIMA reflected the fish availability; and (3) appropriate marine mammal management with respect to FIMA and the EBFM objectives.

The material collected through the literature searches resulted in total of 221 selected papers. We systematically categorised the literature collected as papers that were relevant for field observation methodology (including habitat modelling, $n = 33$), dietary studies ($n = 72$), modelling approaches ($n = 63$), FIMA implications for fish availability and prey–predator dynamics ($n = 25$) and marine mammal management associated with FIMA and EBFM ($n = 28$). A full list of the selected papers is available in Table S1.

3. THE COMPLEXITY OF MARINE MAMMAL–FISHERIES BIOLOGICAL COMPETITION

3.1. Spatial, temporal and resource overlap as indicators of biological competition

Firstly, to determine marine mammal–fisheries spatial and temporal overlap, information on marine mammal distribution and abundance is primarily acquired through systematic land- or boat-based observations (see Godwin et al. 2016, Vincent et al. 2017), and large scale and aerial surveys of vast marine areas frequented by cetaceans as well as seal and sea otter haul out sites (e.g. Huber et al. 2001, Laidre et al. 2001, Bodkin et al. 2002, Lonergan et al. 2007, Bauer et al. 2015, Hammond et al. 2013, 2017). Furthermore, tagging animals with radio, GPS or satellite loggers (e.g. Tinker et al. 2007, 2008, Cronin et al. 2012, Oksanen et al. 2014, Godwin et al. 2016) or attaching cameras (colloquially ‘critter-cameras’; see Bowen et al. 2002, Parrish et al. 2008) allows researchers to track and monitor marine mammals’ foraging ranges, feeding behaviours and success in the wild. In some cases, tracking tagged commercial fish species can reveal their potential predators (see Wahlberg et al. 2014). Unmanned aircraft systems (UAS) or drones represent a highly effective tracking and monitoring tool due to their cost-effectiveness, practicality and low-noise interference (Linchant et al. 2015, Christie et al. 2016). Ultimately, information gathered through various methods of distance sampling allows researchers to further estimate marine mammal distribution and extent of feeding area ranges using various model designs (e.g. SCANS 2006a,b, Thomas et al. 2010, Bailey et al. 2014). Apart from population-level data, information on individual variation in distribution, feeding behaviour and foraging strategy can be acquired through photo-identification using a photographic record of an individual’s unique morphological characteristics, such as

marks, notches, skin or nose scars, as well as the specific pigmentation typically found on the ventral part of the body or fluke (Lee et al. 2009, Urian et al. 2015). Alternatively, data collected through interviews with fishermen can provide an indication of marine mammal occurrence, feeding behaviours and feeding on fish aggregates commercially important to fisheries (see Weise & Harvey 2005, Alves et al. 2012, Gonzalvo et al. 2014).

Mapping of the spatial, temporal and resource overlaps has revealed that most fisheries and marine mammal encounters are concentrated along coastal areas in the Northern Hemisphere, particularly in those areas characterised by strong upwelling events (Kaschner et al. 2001). This is reportedly significant for small marine mammal species such as dolphins, porpoises and seals, whilst less or no spatial and temporal overlap is noted for baleen whales that forage in deeper oceanic waters (Kaschner et al. 2001, Kaschner 2004). Here, the validation of resource overlap between fisheries and marine mammals relies on field observation, but also dietary studies. Traditional qualitative and quantitative approaches for studying diet in marine mammals include analyses of stomach contents, fatty acids content in the blubber and stable isotopes in muscle tissue (Pierce & Boyle 1991, Pierce et al. 2004), and faecal analysis (Pierce & Boyle 1991). Since marine mammal species exhibit a diverse range of foraging strategies and prey selectivity, ranging from a general and opportunistic to a more specific prey preference, dietary studies are crucial for determining trophic levels (see Kaschner et al. 2004). A species' trophic level describes its position with respect to other organisms as well as indicating the qualitative and quantitative nature of their relationship (reviewed in Young et al. 2015). A lingering problem, however, in marine mammal dietary studies is small sample sizes, whereby accurate estimates in diet studies become possible only for species or regions where the sample sizes are adequate (Pierce et al. 2004). Samples of stomach contents, muscle and fat tissue are primarily acquired from bycatch or stranded animals (Pierce & Boyle 1991), but also from hunted animals during commercial whaling (e.g. Olsen & Holt 2001, Johnson et al. 2016), aboriginal subsistence (e.g. Castellini 2000) or 'scientific' (e.g. Folkow et al. 2000, Haug et al. 2002, Konishi et al. 2014, Johnson et al. 2016) whaling. It is important to note that dietary contents can significantly differ depending upon the origin of the sample (see Evans et al. 2003, Hernandez-Milian et al. 2015). Moreover, the non-random sampling as well as the health status of animals used for stomach content

analyses might affect the interpretation of results (see Pierce et al. 2004 for more biases).

To overcome such uncertainties in trophic-level determinations, dietary methods are often combined with one another or various methods of marine mammal observation (see summary in Table 1), whereby stomach content analyses are combined with stable $^{14/15}\text{N}$ analysis, or when determining habitat fidelity, $^{12/13}\text{C}$ analysis (Pierce et al. 2004). Stable isotope analysis is applied to muscle or blubber tissue in cetaceans and vibrissae in seals and sea otters. Since stable isotope analysis lacks detailed dietary information, it cannot provide information on the prey species recently consumed (Pierce et al. 2004, Newsome et al. 2012, Scheinin et al. 2014). Dietary studies occasionally reveal new prey species in a marine mammal diet (see Gladilina & Gol'din 2014) and allow us to determine marine mammal prey selectivity or detect a shift in prey. More importantly, it is often challenging in marine mammal dietary studies to discern whether a change in diet occurred due to prey availability, seasonality, habitat, population density-dependent or ontogenetic/individual behavioural differences (see Tinker et al. 2008 using sea otters as an example). For instance, female Californian sea otters show a significantly diverse range in prey specialisation compared to males, which increases with a reduction in the habitable coastline (Estes et al. 2003, Elliott Smith et al. 2015). Interestingly, studies exploring killer whale populations that specialise in preying upon other great whales have identified a switch to a sea otter and Steller sea lion diet (Mizroch & Rice 2006), and grey seals have been observed to switch from preying upon fish to harbour seals and porpoises (see van Bleijswijk et al. 2014, van Neer et al. 2015), which might be explained by depletion of the original primary prey or individual prey preferences.

Prey variation related to distribution and abundance can play a crucial role in the prey choice of pinnipeds (Laake et al. 2002, Lundström et al. 2010) as well as sea otters (Laidre & Jameson 2006). Standard faecal analysis represents the most common method used in determining diet composition amongst pinnipeds. It relies on hard parts in faecal samples, such as otoliths, which are used to identify prey as well as for quantitative fatty acid signature analysis (QFASA) (see Table 1 for examples). For instance, using historic faecal analysis along with a model showing the frequency of size-specific portions allows a reconstruction of eaten biomass that aids determination of the occurrence of salmon in harbour seal diet (see Laake et al. 2002). However,

Table 1. Examples of studies and methods used for investigating marine mammal diet as well as marine mammal–fisheries resource overlap and potential for biological competition according to marine mammal taxonomic groups. QFASA: quantitative fatty acid signature analysis

Marine mammal group	Applied methods							Examples of study case (study/sampling area)
	Field observation methodology	Stomach content analysis	^{14/15} N analysis	^{12/13} C analysis	Fatty acid analysis	Faecal analysis	Other	
Sea otters	+	–	–	–	–	+	Tagging, aging	Watt et al. (2000) (Alaska, USA, S Bering Sea)
	+	–	–	–	–	–	Tagging, capture–recapture	Estes et al. (2003) (California, USA, NE Pacific)
	–	–	–	–	–	+	–	Kornev & Korneva (2006) (Kamchatka, Russia, NW Pacific)
	+	–	–	–	–	–	–	Laidre & Jameson (2006) (Washington, USA, NW Atlantic)
	+	–	–	–	–	–	Biologging	Tinker et al. (2008) (California, USA, NE Pacific)
	+	–	–	–	–	–	Tagging	Tinker et al. (2007) (California, USA, NE Pacific)
	+	–	–	–	–	–	Photo ID	Lee et al. (2009) (Alaska, USA, N Pacific)
	–	–	+	+	–	–	–	Newsome et al. (2009, 2010) (California, USA, NE Pacific)
	–	–	+	+	–	–	Bayesian mixed model	Newsome et al. (2012) (California, USA, NE Pacific)
	+	–	–	–	–	–	–	Larson et al. (2013) (SE Alaska, USA, N Pacific)
	–	–	+	+	–	–	–	Tyrrell et al. (2013) (in captivity, USA)
	–	–	+	+	–	–	–	Elliott Smith et al. (2015) (California, USA, NE Pacific)
Pinnipeds	–	–	–	–	+	–	–	Laake et al. (2002) (Columbia River, NE Pacific)
	–	–	–	–	–	+	–	Sinclair & Zeppelin (2002) (Bering Sea, N Pacific)
	–	–	–	–	+	–	Attached cameras	Iverson et al. (2004) (in captivity, Canada)
	–	–	–	–	+	–	–	Beck et al. (2007) (E Canada, NW Atlantic)
	–	+	–	–	–	–	–	Lundström et al. (2007, 2010) (Sweden, N and Central Baltic Sea)
	–	+	–	–	–	+	Bayesian approach	Sinclair et al. (2008) (Central Bering Sea, N Pacific)
	–	–	–	–	–	+	DNA barcoding	Deagle et al. (2009) (SE Australia, SW Pacific)
	–	–	–	–	–	+	–	Huisamen et al. (2012) (SW Africa, SE Atlantic)
	–	–	+	+	+	–	GPS telemetry	Waite et al. (2012) (E Russia, NE Pacific)
	–	–	–	–	–	–	DNA barcoding	Deagle et al. (2013) (in captivity, USA)
	+	–	–	–	+	–	–	Meynier et al. (2014) (New Zealand, NW Pacific)
	–	–	–	–	–	–	DNA barcoding	Hui et al. (2017) (SE Japan, NW Pacific)

Table 1 (continued)

Marine mammal group	Applied methods							Examples of study case (study/sampling area)
	Field observation methodology	Stomach content analysis	$^{14/15}\text{N}$ analysis	$^{12/13}\text{C}$ analysis	Fatty acid analysis	Faecal analysis	Other	
Pinnipeds	–	–	+	+	–	–	–	Sepúlveda et al. (2017) (S Chile, SE Pacific)
Pinnipeds + toothed whales	–	+	–	–	–	–	DNA barcoding	Méheust et al. (2014) (NW France, NE Atlantic)
	–	+	+	+	–	–	–	Franco-Trecu et al. (2017) (Uruguay estuary, SW Atlantic)
Toothed whales	–	–	+	+	–	–	Heavy metal measurements	Das et al. (2000) (SW France, NE Atlantic)
	–	+	–	–	–	–	–	de Oliveira Santos et al. (2002) (SE Brazil, SW Atlantic)
	–	–	–	–	–	–	Analysis of morphological data, lactation; feeding observations	Kastelein et al. (2002) (in captivity, UK)
	–	+	–	–	–	–	–	Barros et al. (2004) (Hong Kong, S China Sea)
	–	+	–	–	–	–	–	Spitz et al. (2006) (NW Spain, NE Atlantic)
	–	+	–	–	–	–	–	Fernández et al. (2009) (Canary Islands, NE Atlantic)
	+	+	–	–	–	–	–	Bearzi et al. (2010) (W Greece, E Mediterranean)
	–	–	+	+	–	–	Genetic analysis	Fernández et al. (2011) (NW Spain, NE Atlantic)
	+	+	+	–	–	–	–	Meissner et al. (2011) (E France, NW Mediterranean)
	–	–	+	+	–	–	–	Méndez-Fernandez et al. (2012) (NW Spain, NE Atlantic)
	–	+	–	–	–	–	–	Gladilina & Gol'din (2014) (S Ukraine, Black Sea)
	–	+	–	–	–	–	–	Dede et al. (2015) (W Turkey, E Mediterranean)
	–	+	–	–	–	–	–	Hernandez-Milian et al. (2015) (Ireland, NE Atlantic)
	+	+	–	–	–	–	Monte Carlo resampling	Spitz et al. (2017) (W France, NE Atlantic)
Baleen whales	–	–	–	–	–	–	DNA barcoding	Jarman et al. (2002) (S Australia, SE Indian Ocean)
	–	+	–	–	–	–	–	Konishi et al. (2014) (Ross Sea, E Antarctica)

the disadvantage of using standard faecal analysis lies in potentially under- or overestimating the representation of fish otoliths found in faeces due to a highly digested stage of prey (see Dellinger & Trillmich 1988 for details). By contrast, QFASA detects and measures the unique signatures of fatty acids in prey samples and carries a demonstrated

high accuracy in prey species identification (see Iversen et al. 2004).

Molecular or DNA barcoding of prey species is enjoying increasing use in prey identification and, when combined with stomach content analysis, can assist in identifying potential resource overlap with fisheries (see Méheust et al. 2014). This rather non-

invasive method has been used to identify prey species for whales, dolphins and pinnipeds (Jarman et al. 2002, Parsons et al. 2005, Méheust et al. 2014). DNA barcoding has proven particularly useful in the identification of the soft parts of highly decomposed prey (see Deagle et al. 2009) or damaged fish otoliths found in samples of faeces, vomited food (e.g. from seals) or the stomach contents of dead animals (King et al. 2008, Dunshea 2009). However, DNA barcoding alone is insufficient in quantitative analyses of diet composition since variation in prey proportions amongst different DNA sequencing runs can occur due to factors such as the sequencing direction and quality amongst different species (see Deagle et al. 2013). DNA barcoding is nonetheless particularly useful in dietary studies of baleen whales that consume small-sized or quickly digestible prey such as krill (e.g. Jarman et al. 2002). Furthermore, in the absence of hard or uniquely discernible parts of the ingested prey, the detection and quantification of krill, particularly crustaceans, must rely on prior knowledge of the marine mammal diet as well as optimised DNA sequencing through improved primers and minimising biases originating from variation in DNA amongst conspecifics and different species (King et al. 2008, Dunshea 2009).

Using the data available on marine mammal abundance, distribution, diet composition and foraging strategies, spatial models can be applied to project the range of a foraging habitat and, thus, estimate the potential of spatial, temporal and resource overlap (see Doniol-Valcroze et al. 2012). However, changing environmental conditions and human activities (i.e. prey depletion) can reduce the reliability of such models and yield unrealistic estimates whilst insufficiently accounting for the effects of marine mammal–fisheries biological competition on fish availability (Santos et al. 2013). Under conditions of prey depletion, marine mammals might rely on other food sources such as fish farms (see Sepúlveda et al. 2017, Piroddi et al. 2011) or migrate in search of better feeding grounds (Santos et al. 2002, Bearzi et al. 2006, Scheinin et al. 2014). Moreover, the prey quality, an important factor in prey selection (Bowen et al. 2002), can greatly affect the range of distribution and site fidelity of, for instance, cetaceans due to the significant relationship between diet quality and cost of living (see Spitz et al. 2012). Specifically, cetaceans with high metabolic costs, such as the common dolphin and harbour porpoise *Phocoena phocoena* will develop adequate foraging strategies and, if necessary, forage more to satisfy their need for energy-rich prey. By contrast, sea otters adopt diverse behav-

ioural responses and foraging strategies under high intraspecific competition as well as depending upon prey population density (see Tinker et al. 2007, 2008).

In order to understand the metabolic needs of marine mammals it is important to obtain data on their energetic requirements which, in most cases, stems from studies of marine mammals in captivity. Obtaining information on energetic requirements from marine mammals in the wild can be difficult due to unpredictable environmental and working conditions as well as their shy and elusive nature (Kastelein et al. 2002, Lockyer 2007). Sea otters are, however, an exception from this rule since most of their activities can be observed on the surface or at haul-out sites (see Finerty et al. 2009 for field metabolic rate estimations in wild sea otters). However, studying marine mammals that can be held in enclosed facilities provides a controlled environment where we can observe changes in food intake due to season, sex or age (e.g. Kastelein et al. 2002), energetic requirements (e.g. Rechsteiner et al. 2013) and feeding behaviours (e.g. Levermann et al. 2003). Estimates for daily or annual energy intake, metabolic rates and the length–weight relationship, for instance, obtained from animals in captivity allow us to make preliminary estimates of predation (see Santos et al. 2014). Moreover, research on animals in captivity has also been used to test the reliability of certain dietary methods or to improve such methods (e.g. Iverson et al. 2004, Parsons et al. 2005, Dunshea 2009, Deagle et al. 2013, Tyrrell et al. 2013). Energetic requirements measured in captivity, however, can underestimate the energetic requirements of wild and highly migratory marine mammals (Lockyer 2007), making further estimates such as those quantifying predation rather difficult. However, through the development of more sophisticated bio-logging technology, direct measurements of different energetic parameters on wild-ranging and large marine mammals are becoming increasingly reliable (see Bograd et al. 2010). Information about energetic requirements together with population size, structure and diet can be used to quantify predation, enabling a better estimate of the natural mortality of the fish species and can be used to minimise uncertainties in fish stock assessments.

3.2. Modelling approaches: connecting fish, marine mammal and fisheries dynamics

Diverse model-based approaches have emerged as a response to the questions regarding marine resource availability and management, as well as the

biological and ecological characteristics of target species, populations, and entire ecosystems that can change under a variety of pressures of an anthropogenic or environmental origin. To that end, model-based approaches can be applied to disentangle factors and processes driving fisheries and marine mammals towards biological competition (Pierce et al. 2004, Plagányi 2007) as well as to explore potential functional and structural changes of the ecosystem under marine mammal–fisheries biological competition (e.g. Morissette et al. 2006). The development of models addressing marine mammal–fisheries interactions can be elegantly presented: starting from a simple question of ‘who eats what?’ to ‘who eats how much of what’ and finally, ‘who eats how much of what where’ (see Kaschner & Pauly 2005). While models integrating marine mammal–fisheries interactions have been exhaustively addressed elsewhere (see Harwood & McLaren 2004, Plagányi 2007, ICES 2015), here we focus our attention on the widely used model-based approaches that contribute to an understanding of prey–predator dynamics and marine mammal–fisheries biological competition. The models presented here account for 1- or 2-way interactions, whilst encompassing the relevant trophic levels. We present these models as follows: (1) extended single-species assessment models (ESAM); (2) multispecies, minimum realistic models (MRM), such as Multi-species model for the Barents Sea (MULTSPEC) and Globally applicable Area Disaggregated General Ecosystem Toolbox (GADGET); (3) Models of Intermediate Complexity for Ecosystems assessments (MICE); (4) bioenergetics models; (5) individual- or agent-based models (IBM or ABM) such as OSMOSE and INVITRO; and (6) dynamic ecosystem or end-to-end models (e.g. Atlantis, Ecopath with Ecosim or EwE). Table 2 summarises the main characteristics and suitability of these models with respect to marine mammal–fisheries biological competition.

In general, the initial steps addressing marine mammal–fisheries interactions rely on ESAMs that integrate predation simply as a component of natural mortality or describe it as an analogue to pressure from fishing (see Plagányi 2007). In the initial applications of ESAM in European waters, a simple combination of single- and multispecies models explored the potential interaction between commercially important fishing stocks (i.e. cod, capelin *Mallotus villosus* and shrimp stocks) and 3 species of baleen whales in Icelandic waters (Stefánsson et al. 1997). Similarly, the MULTSPEC model used in studies of the Barents Sea allowed observation of the direct and

indirect effects of fisheries and marine mammals—that is, minke whale and harp seal *Phoca groenlandica*—on 3 commercial fish species: cod, capelin and herring (Bogstad et al. 1997). Whilst the model's assumptions did not allow for reliable quantification of fish removal by the baleen whales, it demonstrated that the marine mammals studied notably contribute to the natural mortality of fish and, if ignored, the future fish catches might be underestimated.

Yet, such models should be used with caution, since merely including marine mammals in initial fish stock assessment models does not adequately take into account differences in life history and ecology of fish and marine mammals (Morissette & Brodie 2014). For instance, combining multi-species functional response (MSFR) and the Bayesian approach can be used to quantify fish removal by marine mammals, providing a better description of the predator's choice of prey whilst accounting for prey availability (see Smout et al. 2014).

MRM models, such as Scenario Barents Sea (SCENARIO), BOREal Migration and CONsumption model (BORMICON), GADGET and Stochastic Multi-Species model (SMS), represent practical tools for addressing trophic interactions between fish stocks and marine mammals due to their minimal data requirements (Plagányi 2007, ICES 2015). In addition to the ESAM models, MULTSPEC, SCENARIO, BORMICON and SMS (see Schweder et al. 2000, Lewy & Vinther 2004, Lindstrøm et al. 2009, ICES 2017), GADGET has been applied to explore fish–marine mammal dynamics in the Norwegian and Barents seas (e.g. Howell & Bogstad 2010). Aside from the single-species assessments of several European fish stocks (e.g. Cerviño et al. 2009, ICES 2016), GADGET has also been used in multispecies contexts, such as the modelling of Icelandic minke (Elvarsson 2013, Elvarsson et al. 2013) and fin whale (Elvarsson 2014) populations, as well as to address northeast Atlantic toothed whale populations, that, for the first time, consisted of common and bottlenose dolphins (Saavedra et al. 2014, Saavedra 2017). Other study cases relying on MRM models worth noting have focussed on the Barents Sea, Antarctic waters and Celtic Sea (see Tjelmeland & Lindstrøm 2005, Mori & Butterworth 2006, Houle et al. 2016). These studies provided better insights into predation pressures experienced by juvenile and adult-stage fish, and the indirect effects of their respective fisheries on predators as well as the concomitant community.

MICE models, similar to MRM models, were developed to adequately encompass the minimally required complexity of ecological, environmental and

Table 2. Summary of the main models addressing direct and indirect marine mammal–fisheries biological competition in harvested ecosystems, in order of increasing complexity and number of trophic interactions (direction depicted by the grey arrow). Models differ based on the primary characteristics, type of prey–predator interactions, ‘efficient’ vs. ‘hungry’ predator (according to Plaganyi 2007) and support to decision-makers to achieve the EBFM objectives. An ‘efficient’ predator forages and feeds until satiated while a ‘hungry’ predator continually feeds

Model category (abbreviation/acronym)	Primary model characteristics and application	Prey–predator interactions and predator function	Supporting EBFM objectives
Extended Single-species Assessment Models (ESAM)	<ul style="list-style-type: none"> - extended fisheries assessment models - minimal biological processes included 	<ul style="list-style-type: none"> - 1-way interaction where predators affect fish - ‘efficient’ predator - predation included as an outside driver similar to a ‘fishing fleet’ 	<ul style="list-style-type: none"> - predation quantification depends on model assumptions - yield preliminary understanding of fisheries–marine mammals dynamics
Multispecies Minimum Realistic Models (MRM)	<ul style="list-style-type: none"> - mainly an extension of MSVPA - age-length structured, addressing multiple fleets and fishing areas - context and system oriented - minimal inclusion of population dynamics as well as operating on minimum data input 	<ul style="list-style-type: none"> - 1- or 2-way interaction - apply various functional responses based on available information on predator abundance, diet composition and consumption estimates - primarily an ‘efficient’ predator, although GADGET has both - prey and predator densities can be limited by their carrying capacities 	<ul style="list-style-type: none"> - address direct and indirect effects of fisheries on fish and predators - used more for theory testing and less for fisheries management (except for GADGET)
Models of Intermediate Complexity for Ecosystems assessments (MICE)	<ul style="list-style-type: none"> - from single-species to ecosystem models - similar to MRM, ecosystem and context specific - can include a minimum of ecological, environmental, management and socio-economic components 	<ul style="list-style-type: none"> - 2-way interaction - ‘efficient’ predator - predator linked, for instance, to prey survival or reproductive success - various functional responses used depending upon available data on predator diet composition and prey preference - prey and predator densities can be limited by their carrying capacities 	<ul style="list-style-type: none"> - aid testing scenarios of different biological, environmental, managerial and socio-economic parameters - provide a tool to form strategic and tactical managerial actions - first-level modelling that considers stakeholders’ opinion
Bioenergetic models	<ul style="list-style-type: none"> - include 1 to 7 species - based on the species-specific energetic or allometric trophodynamics of the individual species - at a minimum, basic biological and diet consumption data are needed while other energetic parameters can be estimated 	<ul style="list-style-type: none"> - account for individual variability in prey–predator dynamics - convenient when only biomass data on prey/predator are available - ‘efficient’ and ‘hungry’ predator 	<ul style="list-style-type: none"> - provide estimates for the energetic requirements as well as quantifying predation with regards to the prey and predator energy uptakes - consider the ecosystem’s energy budgets and flow - generate projections of the fish availability to fisheries and predators
Agent-Based Models or Individual-Based Models (ABM or IBM)	<ul style="list-style-type: none"> - multispecies to ecosystem models - follow the individual’s growth, reproduction and survival - an individual has a critical effect on the system dynamics - some are more suitable for fish predators (e.g. OSMOSE) from single-species to whole ecosystem models 	<ul style="list-style-type: none"> - account for individual variability in prey–predator dynamics - in OSMOSE, predation is typically a function of prey size and the spatial co-occurrence of predator and prey - ‘hungry’ predator 	<ul style="list-style-type: none"> - as ecosystem models, provide insight into the direct and indirect effects of biological competition - allow consideration of a combination of anthropogenic pressures to facilitate decision making
Ecosystem or end-to-end	<ul style="list-style-type: none"> - dynamic, aggregate state and/or spatial models - account for the entire marine trophic web and geochemical processes - include size and/or age structures - data-wise and computationally most demanding models 	<ul style="list-style-type: none"> - apply various functional responses describing the predators’ response to prey population trends (e.g. ‘foraging arena’ in Ecosim), but also prey vulnerability to predator and refuge - primarily ‘efficient’ predator 	<ul style="list-style-type: none"> - most successful in accounting for non-target species - as ABM, provide insight into the impact of the biological competition on the ecosystem level within a socio-economic context - consider a variety of anthropogenic pressures

anthropogenic components in order to provide support to decision-making processes in fisheries and conservation management (reviewed in Plagányi et al. 2014). Alongside ESAMs, MRM models as well as ecosystem and specific IBM (i.e. INVITRO) models, the primary characteristics of MICE models render them suitable for management strategy evaluation (MSE) approaches that include scientific recommendations and can verify the success of proposed management actions (see Plagányi et al. 2014). However, in comparison to MRM, MICE models enable more realistic and applicable recommendations for management given the inclusion of lower trophic levels as well as non-target species (Plagányi et al. 2014, Punt et al. 2016). One such example stems from the study addressing the Californian Current Ecosystem (CCE) where the direct impact of fisheries was estimated for 2 target foraging fish species, 1 non-target species and ‘other’ prey species. As such, an exploration of the indirect fisheries effect on the California sea lion and brown pelican *Pelecanus occidentalis* demonstrated, in the context of CCE, a lack of information on the prey–predator dynamics with regards to predator-specific demographic trends and prey sensitivity to environmental factors (see Punt et al. 2016).

Researchers often use bioenergetic models to compensate for the lack of data on the energetic requirements of wild marine mammals and enable estimates of species-specific energetic requirements for both single- and multispecies interactions (Koen-Alonso & Yodzis 2004, 2005, Plagányi 2007). For instance, energetic requirements and annual prey biomass were estimated for the Atlantic bottlenose population (Bejarano et al. 2017) to determine the impact of marine mammals on fisheries’ success (e.g. Read & Brownstein 2003), which also proved useful for conservation purposes (e.g. Fortune et al. 2013). In the Gulf of Alaska, the magnitude of biological competition between Steller sea lions and fisheries was assessed by comparing predators’ annual energetic requirements and fish availability under various fishing regimes (Cornick et al. 2006). Bioenergetics models assist in quantifying predation pressure and, in some cases, form an integral part of a tailored approach aiming to project energetic requirements based on fish and marine mammal species as well as the concomitant fisheries (e.g. Bjørge et al. 2002, Forcada et al. 2009). Inferring daily energetic requirements, the caloric value of prey and the abundance of killer whales that prey upon sea otters and Steller sea lions indicates that these predators do not have a sufficiently strong prey removal to induce significant

declines in the abundance of sea otters and sea lions (see Williams et al. 2004).

The multispecies model INVITRO allows for the evaluation of management strategies and their effects on ecosystem dynamics (Plagányi 2007). INVITRO and other IBMs rely on true individuals, whilst ABMs apply ‘individuals’ representing conceptual units, that is, fishing fleets, schools or various subsets of a population (Plagányi 2007, ICES 2015). By contrast, OSMOSE (Object-oriented Simulator of Marine eco-System Exploitation) is an ABM and MSE model (ICES 2015). Whilst OSMOSE is a biomass model and shares similarities with specific ecosystem models (e.g. Ecopath), in contrast to INVITRO, it limits the inclusion of the top trophic levels (see Plagányi 2007). Furthermore, whilst suitable for MSE, OSMOSE and INVITRO remain more sensitive and responsive to the level of specific functional groups exposed to fishing or other pressures than on the ecosystem level. This is specifically corroborated when compared to, for instance, Atlantis or EwE (see Travers et al. 2010, Forrest et al. 2015). Other examples of recent studies using IBM include models developed to address specific case studies, such as the ecophysiological IBM simulating energy intake and expenditure amongst individual female Weddell seals *Leptonychotes weddellii* (see Beltran et al. 2017). Combining a bioenergetics model with species-specific prey selectivity and behavioural traits as well as female seal life histories, this IBM allows for a more in-depth understanding of the individual contribution to the energetic budget and population requirements.

From end-to-end models, researchers agree that Atlantis and EwE currently represent the best approaches to addressing complete trophic webs of exploited ecosystems and marine mammal–fisheries biological competition (Plagányi 2007, ICES 2015, Villasante et al. 2016). As encompassing as they are, ecosystem models in general represent computationally intensive and data-demanding models in comparison to ESAM and MRM, although attempts to minimise these trade-offs exists (see Prato et al. 2014 for EwE). Furthermore, complex ecosystem models can potentially underestimate key functional groups (e.g. top trophic levels) due to limited or unreliable data, rendering their application for management purposes quite difficult (Morissette & Brodie 2014, Goedegebuure et al. 2017). Atlantis, for instance, is a spatially explicit model encompassing a wide range of components in a marine ecosystem, from biophysical and operational, fisheries-related components to socio-economic characteristics (Plagányi 2007, ICES 2015). Atlantis has been used extensively in the

northwest Atlantic to test for the effects of pinniped predation and fisheries on demersal fish stocks (Link et al. 2011). Similarly, Atlantis was applied in other regions of the world to explore topics such as the benefits of compliance to different fishing regulations in the Northern Gulf of California ecosystem and fisheries (Ainsworth et al. 2012), to identify key indicators for ecosystem-based management of the southern Benguela ecosystem (Smith et al. 2015) and to verify potential fishery losses under specific conservation measures needed for the survival of the critically endangered vaquita *Phocoena sinus* (Morzaria-Luna et al. 2012).

EwE, a dynamic ecosystem model, shares structural similarities with Atlantis and typically contains 2 components—the Ecosim and Ecopath—or, occasionally, 3 components when Ecospace, its spatial component, is included (Plagányi 2007). Furthermore, Ecopath and Ecosim (Ecopath's mass-dynamic simulation routine) have been used independently or jointly for a wide range of interactions concerning marine mammals, fish, and fisheries within specific ecological, managerial and socio political contexts (Pauly et al. 2000, ICES 2015). In the last 30 yr, EwE has been applied to more than 500 ecosystems (Villasante et al. 2016) and used to address a variety of topics such as resource overlap and interaction between marine mammals and fisheries (e.g. Blanchard et al. 2002, Mackinson et al. 2003, Morissette et al. 2010a,b, 2012), understanding structural and functional properties of food webs in large ecosystems for better ecosystem-based management (e.g. Cornejo-Donoso & Antezana 2008, Torres et al. 2013, Piroddi et al. 2015, Sagarese et al. 2017) as well as for specific cases to determine the effect of fisheries on top predators whilst testing an ecosystem's ability to sustain various fisheries simultaneously (e.g. Goldsworthy et al. 2013). Alternatively, EwE (or its individual components) has been used for various 'custom-made models' for the purpose of, for instance, identifying key functional groups in highly harvested ecosystems (e.g. Coll et al. 2006, 2007), developing a regional end-to-end model exploring the impact of issues such as predation on Steller sea lions by killer whales, fish availability and fisheries on Alaskan ecosystem functioning (see Guénette et al. 2006, Ruzicka et al. 2013), or quantifying marine mammal–fisheries biological competition (including operational interactions) for a more realistic estimation of the impact fisheries on the ecosystem, in particular, on top predators (see Lassalle et al. 2012). EwE specifically assists in revealing the importance of the combined impact of fisheries, predation by grey seals and eutrophication

on shifting regimes observed in the Baltic Sea (see Hansson et al. 2007, Österblom et al. 2007). More precisely, the model revealed a strong top-down control of grey seals on cod as well as cod on sprat (Harvey et al. 2003), whilst the release of predation on cod led to an increase in the abundance of cod as well as a subsequent decrease in cod numbers due to severe fishing intensity and climate change (Österblom et al. 2007).

4. MARINE MAMMAL–FISHERIES BIOLOGICAL COMPETITION IN HARVESTED ECOSYSTEMS

4.1. Considerations of FIMA and trophic interactions in EBFM

Traditional approaches to fisheries management, such as the precautionary approach or maximum sustainable yield (MSY), promote the minimisation of natural and fishing mortality through the regulation of fishing quotas, effort and gear (Pauly et al. 2002). However, these actions appear inadequate, as they propose short-term management actions whilst underestimating the role of ecosystem processes and their integrity in the provision of resources (Lassen et al. 2014). By contrast, EBFM advocates for the importance of balanced exploitation as a means to maintain biodiversity at all levels as well as preserving the balance throughout the food web and ensuring high fishery yields in the future (Leslie & McLeod 2007, Zhou et al. 2010, Garcia et al. 2012). Existing cases of EBFM implementation serve to strengthen its primary principles in preserving marine food web interactions, accounting for the incidental impact of fisheries on the ecosystem (particularly those related to non-target species) as well as considering the socio-economic context of the human demand for fish (see Ruckelshaus et al. 2008). Recognising the observed FIMA in individual fish and the potential adverse effects it could have on prey–predator interactions, EBFM should account for eco-evolutionary processes and their persistent negative consequences (see Jørgensen et al. 2007, Laugen et al. 2014) in order to accomplish a truly holistic approach to natural resource management. By definition, holistic fisheries management should acknowledge all structural levels and processes in an 'ecosystem' and an 'ecosystem' with respect to their independent and coupled effects (see Fowler et al. 2013).

Eco-evolutionary feedbacks in dynamic trophic interactions can pervasively affect all structural levels (Kuparinen et al. 2016); thus, identifying their

implications within the context of EBFM remains critical for the overall structural stability and ecosystem phenology (see Lankau & Strauss 2011, Johansson et al. 2015, Kuparinen et al. 2016). Moreover, from the individual to the population level, the cascading effect of FIMA can ultimately render certain management measures inefficient since it affects the population reference points (see Heino et al. 2013). Whilst several mechanisms of eco-evolutionary processes are recognised (reviewed by Bolnick et al. 2011), the size-selective removal of fish reportedly represents a prevailing pressure driving phenotypic and behavioural trait changes in fish, the latter being more experimentally documented (e.g. Uusi-Heikkilä et al. 2008, Heino et al. 2015). In comparison to the size selectivity of fishing gear, the size selectivity of prey in marine mammal diets has developed through evolutionary time; however, it is also transferable from mother to calf or pup in most marine mammal species (Estes et al. 2003, Etnier & Fowler 2010). Fishing selectivity and intensity can induce different responses, such as in direction of change in individual traits, depending upon whether the fishing pressure is directly applied to growth or maturation, or indirectly, through the selectivity of one trait whilst affecting its associated traits (see Heino et al. 2015). Marine mammals, by contrast, demonstrate a general consistency in prey size selectivity across numerous study cases, targeting fish species of less than 30 cm in body size (see Etnier & Fowler 2010). Despite this, biases may still affect prey selectivity in the marine mammal diet, such as through prey availability as well as intra- and interspecific competition. For instance, when compared to the size selectivity of commercial fisheries within similar spatial, temporal and resource contexts, marine mammals appeared to intentionally target smaller-sized fish (Etnier & Fowler 2010). Elucidating those factors driving marine mammals to target certain prey sizes over others as well as detecting the window of opportunity in terms of prey size for both marine mammals and fisheries poses significant challenges in distinguishing their impact upon potential individual trait changes in fish.

Careful investigation of empirical case studies addressing marine mammal–fisheries biological competition on a lower spatial scale could provide an insight into how the species' life histories as predator and prey affect their responses to fishing pressure as well as the direction and magnitude of eco-evolutionary feedback on an individual level. Alternatively, modelling the coupled effects of fishing and predation, whilst observing life-history and behavioural

traits as well as how these contribute to natural mortality, can predict different trends in individual fish traits. Some recorded trends are: increases in natural mortality accompanying decreases in fish body size, increased growth rates (due to additional risks related to foraging and energy allocations) and increased investments in reproduction (precisely, as a consequence of increased exposure to predation due to reproduction-related behavioural or morphological traits; Jørgensen et al. 2010). At the population level, the effects of predation and fishing may entail greater consequences for fish biomass, recruitment, stock recovery and, ultimately, their management (see Jørgensen et al. 2007, Hutchings 2009). Although some researchers argue that the theoretically estimated rate of evolution in fish is slow (see Andersen & Brander 2009) and the strength of phenotypic plasticity in some fish species can dampen the evolutionary changes in individual traits (see Hidalgo et al. 2014), others highlight the cumulative effect of size-selective fishing that can impair the recovery of population size to its pre-exploited level or completely prevent it (see Kuparinen & Hutchings 2014, Hutchings 2015, Swain & Benoit 2015).

In the increasingly harvested ecosystems, biological competition among marine mammals and fisheries inevitably impacts the connectivity and structure of marine trophic interactions (see Estes et al. 2016). Thus, any disturbance or weakening observed in prey–predator interactions in an ecosystem acts as an indication of structural disruptions caused by fisheries (Pauly et al. 2002). In fact, a body of research has explored the implications of trophic interactions on fisheries' sustainability (Worm et al. 2009). Studies applying IBM, ABM and ecosystem models have significantly contributed to our understanding of prey–predator dynamics, changes in the diet of marine mammals and how these reflect on the stability of the food web. The intensity of biological competition depends upon prey availability and distribution as well as the accessibility of prey to the competitors. Furthermore, prey accessibility will vary depending on the scope of resource overlap between competitors, environmental conditions and the effect of non-target species in trophic interactions (Bogstad et al. 2015). Additionally, we should consider the effects of other relevant ecological processes on EBFM including intra- and interspecific competition for prey among different species of marine mammals. As examples, we can take the case of grey and harbour seal trophic overlap in the North Sea (ICES 2015), as well as the potential of resource competition between marine mammals, fisheries and other mar-

ine megafauna, such as sharks, marine birds and predatory fish (e.g. Huss et al. 2014). For instance, the resource competition between cod, harp seals and minke whales in the Barents Sea was explored considering the availability of shared prey and historic environmental conditions in an attempt to reveal possible mechanisms of the competition (Bogstad et al. 2015). Here, the developmental stage of fish (i.e. juvenile and adult fish) was carefully considered, identifying different susceptibilities and vulnerabilities to specific pressures. Notably, this study highlights the importance of accounting for the different trophic positions occupied by the same individual throughout its development.

Ultimately, understanding the importance and implications of trophic interactions for achieving sustainable fishing and ecosystem functioning not only facilitates achieving the EBFM objectives, but also recovering the current state of any prey and predator populations (e.g. Chadés et al. 2012).

4.2. Benefits of preserving prey–predator dynamics in reaching the EBFM objectives

Regarding the need to manage the negative impact of fishing on the individuals and the ecosystems, harvest balancing that assigns fishing rates proportional to species productivity represents an effective approach to achieving the EBFM objectives (Law et al. 2012). With respect to prey–predator dynamics, preserving ecosystem resilience and functioning becomes feasible through balanced removal of prey and predator (see Tromeur & Loeuille 2017). However, implementing balanced harvesting remains challenging due to the increased fishing pressure on juvenile fish (Burgess et al. 2016) as well as the difficulty associated with measuring the population or individual productivity of the target species (Jacobsen et al. 2014). For instance, higher productivity at the lower trophic levels implies more sustainable fishing at these levels than removing species with a lower productivity at a higher trophic level (e.g. Law et al. 2012). Predator removal through culling programmes stands as an effective means of reducing predator abundance; nonetheless, such programmes offer a short-term solution that does not always result in an increase in the target species population (see Morissette et al. 2012, Houle et al. 2013), since the effects are difficult to project and measure (Bowen & Lidgard 2013). Thus, the scientific community recommends a precautionary approach to managing marine mammals such as the top predators (which also

includes moderate harvesting) to avoid adverse effects on the fish and economic losses for fisheries due to sudden and unregulated predator population increase (see Augé et al. 2012). This occurred in many pinniped populations which, following historical declines, thrived under protection programmes, in some cases leading to increased biological competition with fisheries and commercial fish stock declines (Augé et al. 2012, Marshall et al. 2016).

In addition to marine mammal removal, which can potentially disrupt the finely tuned trophic connectivity throughout the ecosystem, fewer unexpected outcomes might result from ensuring the survival and viability of marine mammal populations (Augé et al. 2012, Garcia et al. 2012, Papastavrou et al. 2017). This requires an adequate ‘package’ of mutually complimentary and synchronised conservation and management measures that could ensure the preservation of the trophic web and long-term, sustainable harvesting. Amongst various actions targeting different species or habitats of interest, the establishment of marine protected areas (MPAs) and the holistic monitoring and management of fish stocks through the appropriate involvement of relevant stakeholders represent steps towards EBFM (Leslie & McLeod 2007, Augé et al. 2012).

In general, MPAs focus on protection of vital breeding and feeding areas, although these are species-specific and can vary depending upon spatial and temporal scales (see Pompa et al. 2011, Scales et al. 2014). While new empirical evidence on the successful application of MPAs in favour of marine mammal protection continues to emerge, such as findings from the Banks Peninsula Marine Mammal Sanctuary in New Zealand (see Gormley et al. 2012), maintaining a balance between exploitation and conservation objectives calls for the long-term monitoring and continuous re-evaluation of the efficiency of applied management actions (Marshall et al. 2016). This also entails inclusion of protective measures for fish stock that not only consider natural predators (see Fanshawe et al. 2003 for sea otters), but also examine potential FIMA or predation effects or both. In the specific case of angling of largemouth bass *Micropterus salmoides*, MPAs appear useful for preventing the loss of phenotypic diversity through the promotion of aggressive behavioural traits, thus ensuring survival of bass through more cautious and aggressive protection of nests (see Twardek et al. 2017). This, however, might not apply to ongoing evolutionary change (see Dunlop et al. 2009 for the potential effects of MPAs for fisheries-induced evolution). In cetaceans, for instance, studies of social

and behavioural traits have demonstrate that baleen whale characteristics—that is, being shy and elusive—have benefited their recent recovery, whilst the rather opportunistic feeding behaviour of toothed whales exposes them to incidental catches by fishing gear, rendering their recovery difficult (see Wade et al. 2012). Because cetaceans exhibit complex social behaviour within their population, focal group or as individuals, conservation measures must account for their social as well as physical well-being since they directly affect the survival and viability of a species, thereby increasing the effectiveness of conservation efforts (Wade et al. 2012, Marshall et al. 2016).

Ensuring sustainable fishing regimes and preserving marine environments are crucial EBFM objectives that require supporting protective acts and legislation, established through collaboration between scientists and relevant stakeholders (e.g. Gleason et al. 2010). Local stakeholders, such as artisanal fishermen with their small communities are tightly connected to fishing activities and possess a rich ethnoecological knowledge of local megafauna providing additional knowledge of historic shifts in abundance, distribution and behavioural patterns of the relevant megafaunal species (see Costa et al. 2012, Zappes et al. 2014). Such interdisciplinary approaches help ensure more effective conservation measures, but also directly involve the most affected stakeholders, such as fishermen and their communities, in decision-making processes that ultimately affect their own livelihood. Additionally, successful coexistence and collaboration amongst fishermen and marine mammals can be of benefit to both, as is the case for the cooperative fishery between artisanal fishermen and the resident bottlenose dolphin population in southern Brazil (e.g. Daura-Jorge et al. 2012).

5. CONCLUSIONS AND FUTURE RESEARCH

Focussing on 2 specific areas, the synthesis of knowledge about marine mammal–fisheries biological competition presented here is purposefully narrowed down and biased towards its focus and approach. However, while the literature gathered here is not fully exhaustive of relevant scientific research, we have striven to present the most representative examples of studies and their methodologies complementing the 2 areas of focus.

Given the long history of human conflicts with marine mammals for commercially viable fish species, the research reviewed here demonstrates the continuous effort to explore the direct and indirect effects of bio-

logical competition. To this end, the notable proliferation of methodology, particularly model-based approaches, has provided insights for studying data-limited ecosystems and species, and investigating the availability of fish for fisheries and marine mammals with respect to the ecosystem characteristics, management objectives and regulations as well as the aims of national or international policies and strategies. Nonetheless, difficulties in obtaining information about marine mammals' choices and the selectivity of prey and, consequently, their adequate representation in currently used assessment models, calls for further improvements to model-based approaches.

Overexploitation, climate change, eutrophication and mismanagement represent some of the main contemporary threats to the global marine environment. Many natural scientists agree that overfishing currently stands as the greatest threat to the sustainability of contemporary marine ecosystems (see Boonstra et al. 2015). However, because climate change directly affects the distribution of species through changes to favourable environmental conditions, the effects of warming need to be directly addressed in the hope of counteracting any damaging effects. A rising number of studies have already demonstrated the potential losses caused by the changing climate vis-à-vis the availability of fish for fisheries, prey and predator demography and their health status as well as the overall feedback on ecosystem functioning (e.g. Harvell et al. 1999, Tegner & Dayton 2000, Schumacher & Kruse 2005, Kovacs et al. 2011, Nye et al. 2013, Konishi et al. 2014).

Given these ongoing threats, advancing towards a holistic EBFM whilst reducing uncertainties regarding FIMA and fisheries' incidental impacts on all structural levels, represents an ambitious but necessary step in managing the biggest threat to marine ecosystems for the preservation of their functioning and services. Latent risks, such as FIMA and eco-evolutionary feedbacks induced by fishing or other coupled pressures, need to be thoroughly accounted for in the long-term forecasting of fish availability. In addition, a specific monitoring strategy could potentially detect changes in individual traits. Alternatively, the protection of key species at the top trophic levels is increasingly supported by relevant stakeholders in the fishing industry. Such supporters increasingly recognise the importance of these species for the long-term sustainability of fishing yields and the stability of the food web that sustains it. To this end, researchers need to provide recommendations and guidelines with a demonstrated feasibility, which primarily includes technical, logistical

and economic feasibility. Moreover, to strengthen the role and credibility of researchers when providing advice, the adoption of the precautionary approach should be warranted since pushing it too far may also lead to mismanagement (see Schweder 2001).

Diminishing fish availability, however, is not the only threat human activities have brought upon marine mammal existence (see Moore 2014). Thus, marine mammal conservation measures should be 'tailored' according to the species-specific life history, site fidelity and foraging habitats, as well as individual phenotypic or behavioural traits based on the selectivity of the threat in question (e.g. bycatch and collisions with ships). Yet, understanding the often entangled processes of marine trophic interactions, selective harvesting and, especially, latent evolutionary changes, under a growing number of other threats, emphasises the significant need for future applied research into ecosystem-based management and conservation. Moreover, whilst the ecological impact of fishing on marine environments can be easily recognised by the general public and relevant stakeholders, preliminary social inquiries illustrate how the evolutionary impact of fishing on fish availability is much more difficult to communicate (see Diaz Pauli & Heino 2013). Given the importance of a holistic approach to EBFM implementation, facilitated by adopting strategic frameworks and legislation as well as encouraging participatory stakeholder involvement, an obvious need exists for further interdisciplinary studies. That is, future interdisciplinary studies should provide a way to effectively address the lack of knowledge and adequate methods to balance human demands for fish whilst simultaneously addressing the obvious necessity of protecting marine resources and their environment.

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